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The role of predation by decapod crustaceans in seagrass ecosystems*

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Abstract

Data from a series of laboratory and field predation experiments using fish and decapod predators from seagrass beds in the Indian River, Florida, USA, indicated that the density of many of the taxonomic groups of seagrass-associated macrobenthos were related in a negative exponential manner to the total density of decapod crustaceans present. Significant regressions were observed in the laboratory and the field experiments for the Amphipoda, Gastropoda, Bivalvia, Polychaeta, Sipunculida, and Tanaidacea, whereas the Isopoda and Nemertinea showed no such relationships. These data emphasize the fact that simplification of intermediate trophic levels in trophic models is unwarranted and may result in failure to recognize important regulatory pathways for seagrass community structure.

Introduction

Seagrass ecosystems are among the most trophically complex ecosystems known (KIKUCHI 1966, KIKUCHI and PERES 1977, LITTLEJOHN et al. 1974, THAYER et al. 1975). This high degree of trophic complexity greatly increases the difficulty in determining which pathways are the critical ones for regulation of the structural properties of the community. Whereas considerable information is now available concerning interactions between the intermediate trophic levels represented by the invertebrate macrobenthos and higher carnivores such as the fishes (KIKUCHI 1966, CARR and ADAMS 1973, LITTLEJOHN et al. 1974, ADAMS 1976, NELSON 1979, STONER 1980), little information is available on important pathways within the intermediate trophic levels themselves.

In the course of examining data collected during experimental studies of decapod and fish predation on seagrass macrobenthos, it was noted that abundances of certain taxonomic groupings of the macrobenthos showed significant negative exponential relationships with the total density of decapod crustaceans present in the various experimental and control samples. This paper presents these results as further evidence for the fact that a significant role is played by the decapod crustaceans in regulating community structure of seagrass macrobenthos. As a result, it is suggested that a considerably less linear viewpoint of seagrass ecosystem trophic structure is required.

Methods

Experimental methods, having been described in detail elsewhere (NELSON 1981), will only be briefly considered here. All field experiments and collection of

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experimental animals were carried out near Link Port in the Indian River, Florida. The physical aspects of this study site have been previously described by YOUNG et al. (1976).

Laboratory experiments used intact cores (15 x 15 x 15 cm) of the seagrass *Halodule wrightii* and sediment which were placed in aquaria. Field experiments used cage structures (50 x 50 x 50 cm, 1 mm mesh) placed in an *Halodule* bed in the Indian River. Both types of experiments ran for 21 days. Species examined as predators were the shrimps *Penaeus duorarum* and *Palaemonetes intermedius*, the crab *Callinectes sapidus*, and the fish *Lagodon rhomboides*. Densities and sizes of the predators used in the various experiments are given elsewhere (NELSON 1981). At the completion of an experiment, samples were sieved on 1 mm mesh, preserved, and all animals counted.

Analysis of data for this paper consisted of the calculation of the regression equations relating the logarithmic abundance of a given taxonomic group to the logarithmic abundance of the total number of decapod crustaceans present using the pooled data from either the laboratory or the field experiments. In cases where regressions were non-significant, treatment means rather than individual sample values are presented for simplicity. Where zeros were present in the data, the log ($x + 0.5$) or log ($x + 1$) transformation was applied as required. In such cases, only the transformed data are presented in the figures. The taxonomic groups for which this relationship was examined are the Amphipoda, Isopoda, Tanaidacea, Gastropoda, Bivalvia, Polychaeta, Nemertinea, and Sipunculida. Lists of the species composing these groups are given elsewhere (NELSON 1981).

Results and discussion

The relationships of the densities of the various taxonomic groups of seagrass macrobenthos to the density of decapod crustaceans in samples from the laboratory and field experiments are shown in Figures 1 and 2, respectively. In all cases, where significant correlations were found, a negative exponential relationship between the two abundances was observed.

Among the crustacean groups, the Tanaidacea showed significant correlations in both laboratory and field data (Figs. 1, 2). *Hargeria repax*, the only species present, is rather small and may therefore be a reasonably-sized prey item for many of the decapod crustaceans. Amphipod density appeared related to decapod density only in the laboratory data (Fig. 1), probably because of the added presence in the field samples (Fig. 2) of several species of small fish (NELSON, in prep.) which commonly feed on amphipods. The isopods, on the other hand, showed no relation to decapod density in either set of samples (Figs. 1, 2). This may be due to behavioral differences of the isopods as compared to the amphipods and tanaids. These include the ability of some species to roll themselves into a tight ball when threatened as well as the tendency of many isopods to be relatively sessile and to cling very closely to the seagrass substratum. Lower predation rates on isopods than amphipods by a small goby has been observed (NELSON, unpublished data), perhaps due to the above factors, and may similarly be operating with respect to the decapods.

The gastropod molluscs showed significant negative correlations between their density and decapod density in both sets of data, whereas the bivalves showed such a relationship only in the field data (Figs. 1, 2). For the bivalves, if the regression is calculated using treatment means rather than individual samples, the correlation coefficient is considerably higher ($r = -0.85$, $p < 0.01$). For both the gastropods and

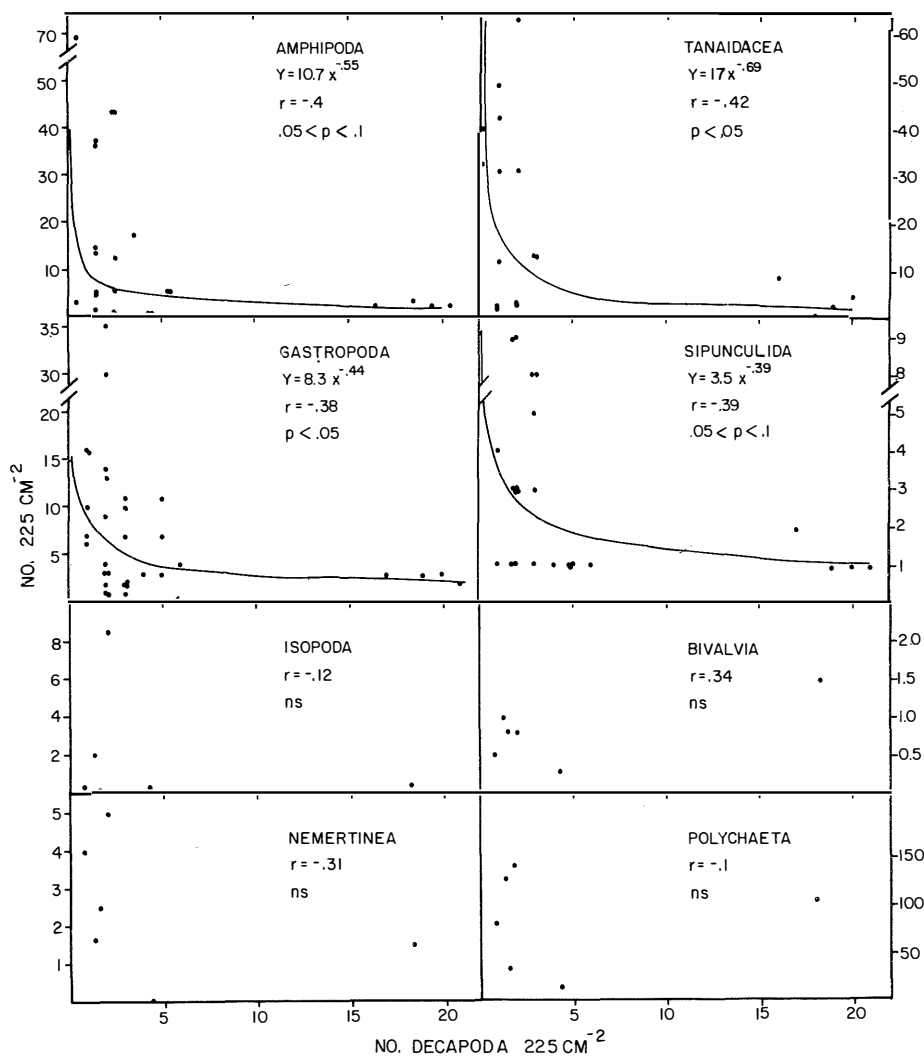


Figure 1

Relationships of the abundances of 8 taxonomic groups of seagrass-associated macrobenthos with the abundances of decapod crustaceans from laboratory experimental samples

bivalves, the most important decapod was the crab *Callinectes sapidus*. For the bivalves, this is clearly shown in Fig. 3, where a significant negative exponential relationship is shown to exist between mean bivalve abundance and mean abundance of *C. sapidus* alone in the field samples. This correlation can account for some 54 % of the variance in mean bivalve numbers within the various treatments.

Abundances of the Sipunculida, represented by the single species *Phascolion cryptus*, showed significant correlations with decapod abundance in both the laboratory and field data (Figs. 1, 2). Density of this species can be affected by both shrimps and crabs despite the fact that it is a cryptic inhabitant of empty gastropod shells (NELSON 1981).

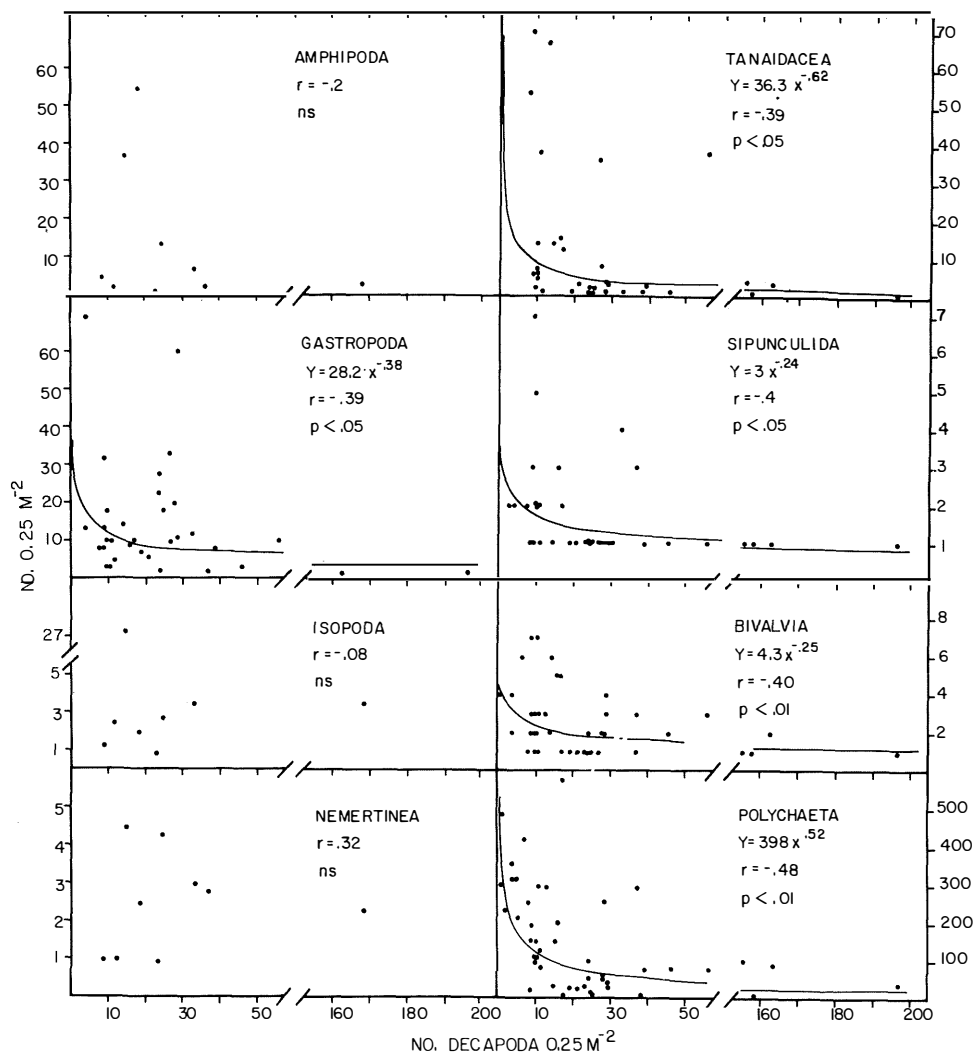
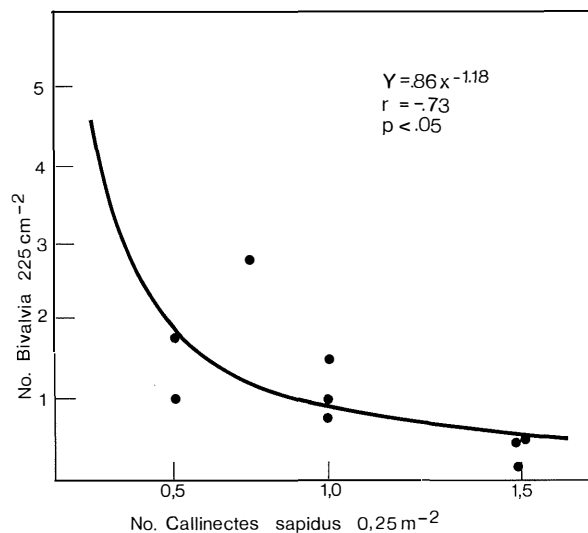


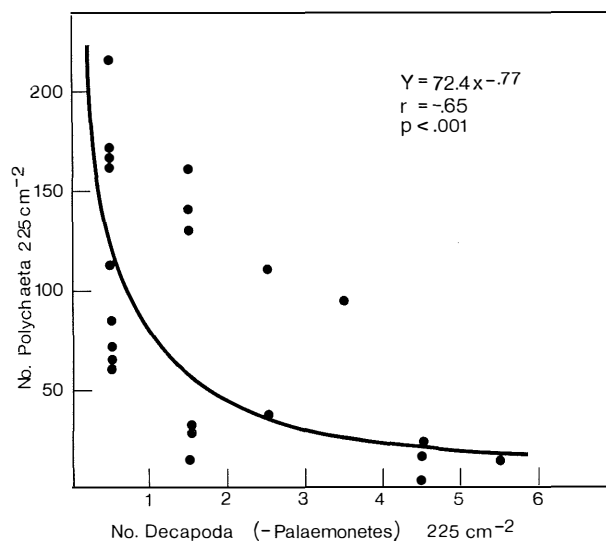
Figure 2

Relationships of the abundances of 8 taxonomic groups of seagrass-associated macrobenthos with the abundances of decapod crustaceans from field experimental samples

Nemerteans, however, showed no relationship to decapod abundances in either laboratory or field data (Figs. 1, 2). Polychaete abundance showed a clear relationship to decapod abundance in the field data (Fig. 2), but no clear pattern in the laboratory (Fig. 1). However, if polychaete abundance in the laboratory samples are regressed with the total abundance of all decapod species except *Palaemonetes intermedius*, a clear negative exponential relationship is seen (Fig. 4). This difference in field and laboratory data is due to the greater presence in the field samples of *Penaeus duorarum*, which has been shown to have a much stronger effect on polychaete density than *Palaemonetes intermedius* (NELSON 1981).

**Figure 3**

Relationship of mean bivalve abundances and mean abundances of the crab *Callinectes sapidus* in field experimental samples

**Figure 4**

Relationship of polychaete abundances and decapod abundances, omitting *Palaemonetes intermedius*, in laboratory experimental samples

Six of the eight major taxonomic groups of seagrass macrobenthos abundantly found in Indian River *Halodule* beds therefore show a significant relationship to abundance of decapod crustaceans. The percentage of the variance of the abundances of these groups which can be explained by this relationship ranges from 14 % to 72 %. That these correlations were obtained in spite of the fact that data were obtained from a

variety of manipulated and control samples spanning a four month period of time is an indication that the processes generating them are of general occurrence within this particular seagrass system.

As was pointed out by DARNELL (1958), trophic studies of complex aquatic communities frequently neglect the interactions among intermediate trophic level components. This is found in studies of seagrass ecosystems where emphasis has tended towards either primary productivity aspects (McROY and McMILLAN 1977) or tertiary consumers such as the fishes (KIKUCHI 1966, KIKUCHI and PERES 1977, LITTLEJOHN et al. 1974, ADAMS 1976). This trend is combined with the tendency of energy flow studies to compress intermediate trophic level components into a more manageable single compartment (e.g. THAYER et al. 1975). Studies of estuarine ecosystems based on gut content analyses (DARNELL 1958, ODUM and HEALD 1972) may also have contributed to the tendency to underestimate the importance of secondary consumer interactions. It must be remembered that although a macrobenthic species may form only a relatively small percentage of the total diet of, for example the decapod crustaceans, this percentage may still constitute a highly significant source of mortality for the preyed-upon species. This may be particularly true for those species already low in abundance for other reasons. The net result has been that most published food webs of seagrass ecosystems tend to be rather linearly hierarchical in nature (Fig. 5, loosely based on KIKUCHI 1966 and LITTLEJOHN et al. 1974). However, evidence is now accumulating which indicates that certain of the intermediate trophic level groups, in particular several of the decapod crustaceans, may exert considerable influence on the species densities of numerous other species of the macrobenthos.

For seagrass ecosystems, considerable experimental work within the Indian River (YOUNG et al. 1976, YOUNG and YOUNG 1977, 1978, VIRNSTEIN 1978, VIRNSTEIN et al., in prep., NELSON, in prep.) has clearly demonstrated that decapod crustaceans as a

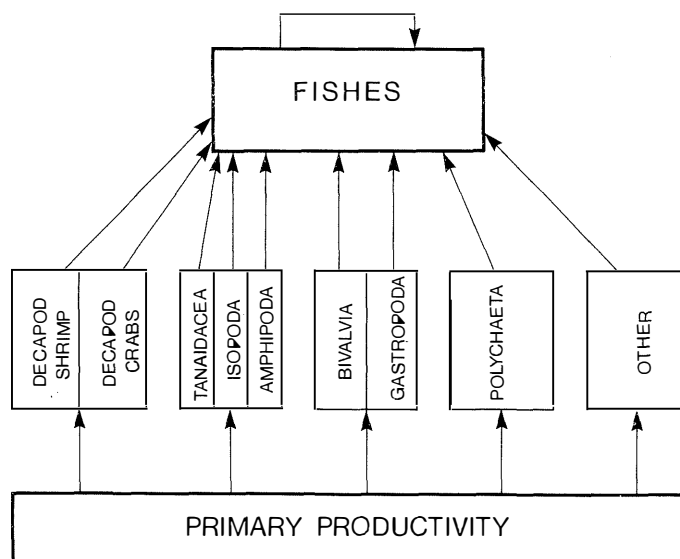
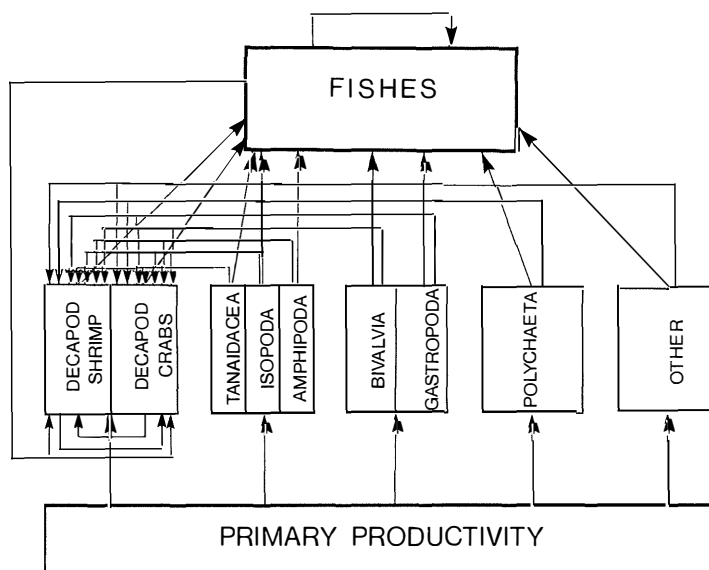


Figure 5

A typical generalized trophic model for seagrass ecosystems

**Figure 6**

A generalized trophic model of seagrass ecosystems modified to indicate the importance of interactions among the components of the intermediate trophic levels

group are of importance in the regulation of species densities of other macrobenthos. Additionally, both REISE (1977) and BELL and COULL (1978) have demonstrated that several species of shrimps are effective predators and/or disturbance agents in muddy sediments and salt marshes, respectively. Such data, including that presented herein, emphasize the fact that within intermediate trophic levels predatory interactions may be important, complex, and not nearly so clearly linear as ordinarily indicated. The actual state of affairs may be more nearly as shown diagrammatically in Fig. 6, and this too is certainly still a major simplification of the important regulatory pathways.

In the face of such trophic complexity, the type of correlation reported in this paper offers some hope of being a useful simplifying relationship for describing the functional interactions of intermediate trophic level groups with other components of the seagrass macrobenthos. The presence of these general relationships suggests that in spite of a bewildering number of potential interspecific interactions in seagrass ecosystems, it may still be possible to identify those particular interactions which may be of central significance to the organization of the community. It appears that at least one of these central factors may be the abundance of shrimps and crabs present in any given seagrass ecosystem.

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